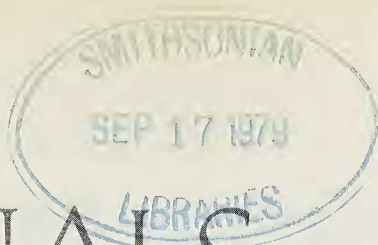


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## GEOMYOID RODENTS FROM THE VALENTINE FORMATION OF KNOX COUNTY, NEBRASKA

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### ABSTRACT

Four heteromyids (*Cupidinus nebraskensis*, *Perognathus furlongi*, *Perognathus troctioansrum*, new species, and "*Diprionomys*" *agrarius*) and a geomyid (*Ligninus* cf. *L. hibbardi*) are recognized from the Crookston Bridge Member of the Valentine Formation, University of Nebraska State Museum locality Kx 110. The large sample of *Cupidinus nebraskensis* collected from this locality provides evidence for the synonymy of *Cupidinus* and *Perognathoides*. The subfamilial assignment of the geomyid is questioned.

The geomyoids present in locality Kx 110 are a combination of Barstovian and Clarendonian species, thus, little can be said concerning the definite age of the Valentine Formation from these forms alone.

### INTRODUCTION

The age of the Valentine Formation of Nebraska (in terms of provincial ages of Wood et al., 1941) has long been argued, with very little understanding of the micromammals from the formation (see Skinner et al., 1968; Webb, 1969; Schultz et al., 1970). In recent years extensive collecting of fossil microvertebrates by means of screen washing by field parties of the University of Nebraska State Museum has been undertaken in the Crookston Bridge Member of this formation. One of the most fossiliferous localities is Annie's Geese Cross Quarry (UNSM locality Kx 110) in Knox County, Nebraska. Voorhies (1971) briefly described the location of this quarry (which he called locality

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"B") and its stratigraphic position. Korth (1979) discussed the taphonomy of this quarry.

This paper will describe a part of the mammalian fauna from Kx 110, the geomyoid rodents. A greater knowledge of this fauna will yield a better understanding of the age of the Valentine Formation in relation to other North American faunas.

Abbreviations used: CM = Carnegie Museum of Natural History; UMMP = University of Michigan Museum of Paleontology; UNSM = University of Nebraska State Museum; N = number of specimens measured; M = mean; SD = standard deviation; CV = coefficient of variation; OR = observed size range. Cusp nomenclature follows Rensberger (1971). Measurements equal the maximum width of the protoloph or metalophid (tra), metaloph or hypolophid (trp), and anteroposterior length (A-P) of measured teeth taken at the base of the crown. A-P measurement on  $P_4$  taken parallel to occlusal surface except for *Lignimus* cf. *L. hibbardi*, which was taken perpendicular to the posterior wall of the tooth. All measurements in millimeters.

#### SYSTEMATIC PALEONTOLOGY

##### Order Rodentia

##### Superfamily Geomyoidea

##### Family Heteromyidae

##### *Perognathus furlongi* Gazin, 1930

(Figs. 1, 2 and Table 1)

Three specimens are referable to this species—UNSM 56300, a complete mandible with all teeth present; UNSM 56301, a maxilla with  $P_4$ – $M_3$ ; and UNSM 56314, a partial right mandible with  $M_2$ – $M_3$ .

The size of these specimens is comparable to that previously recorded for *Perognathus furlongi* (Wood, 1935; James, 1963; Lindsay, 1972). The lower dentition of UNSM 56300 falls into the lower part of the size range of *P. furlongi*, but UNSM 56314 is slightly larger and more nearly approaches the mean sizes of this species (Lindsay, 1972:43).  $P_4$  of UNSM 56300 is below the observed range of size of this tooth in the California sample. This minor difference in size of  $P_4$  cannot be viewed by itself as a diagnostic feature of the Crookston Bridge form in light of the amount of variation of many characters of *P. furlongi* (James, 1963) and the small number of specimens referred to this species (Wood, 1935; James, 1963; Lindsay, 1972).

The lower molars of the UNSM specimens agree in morphology with the referred specimens of *P. furlongi*.  $P_4$ , however, is much shorter anteroposteriorly than in the previously described specimens. The cusps of the hypolophid of  $P_4$  are set well apart as in other specimens of *P. furlongi*. A minor swelling (hypoconulid) occurs between and

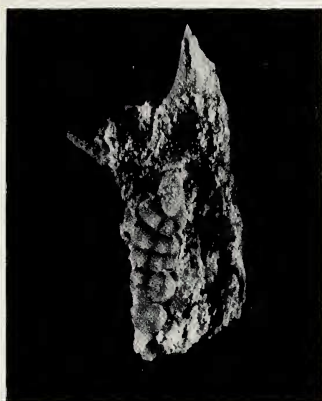


Fig. 1.—*Perognathus furlongi*, stereoview, UNSM 56301,  $RP^4-M^3$ .  $\times 5.25$ .

Fig. 2.—*Perognathus furlongi*, stereoview, UNSM 56300,  $RP_4-M_3$ .  $\times 5.25$ .

Table 1.—Measurements of the dentition of *Perognathus furlongi*.

UNSM no.	P <sup>1</sup>			M <sup>1</sup>			M <sup>2</sup>			M <sup>3</sup>			alveo- lar length
	A-P	tra	trp	A-P	tra	trp	A-P	tra	trp	A-P	tra	trp	
56301	1.42	0.68	1.21	0.87	1.17	1.11	0.70	1.15	1.07	0.70	0.91	0.81	4.15

UNSM no.	P <sub>4</sub>			M <sub>1</sub>			M <sub>2</sub>			M <sub>3</sub>			alveo- lar length
	A-P	tra	trp	A-P	tra	trp	A-P	tra	trp	A-P	tra	trp	
56300	0.68	0.63	0.79	0.86	0.99	1.07	0.80	1.06	1.01	0.72	0.88	0.71	4.03
56314	—	—	—	—	—	—	1.00	1.12	0.98	0.82	0.96	0.72	—

distinct from the entoconid and hypoconid. The two cusps of the meta-lophid are much smaller than those of the hypolophid and positioned closer to the center of the tooth. The anterior cusps are closely appressed against the hypolophid, making the outline of the tooth nearly triangular with a slightly broadened anterior apex.

The upper premolar and molars of the UNSM specimen agree in shape and crown morphology with those in other *P. furlongi*. M<sup>3</sup> appears to be nearly circular in occlusal outline, much more so than is described in published material. This may be a minor variation in tooth morphology and not a specifically distinct character.

*Perognathus trojectionansrum*, new species  
(Figs. 3, 7 and Table 2)

*Perognathus* sp. Klingener, 1968:68.

*Holotype*.—UNSM 56311, right mandible with P<sub>4</sub>–M<sub>3</sub>.

*Horizon and locality*.—Late Barstovian (Miocene) Crookston Bridge Member, Valentine Formation, UNSM locality Kx 110 and Norden Bridge Quarry (UNSM locality BW 106), Brown County, Nebraska.

*Hypodigm*.—Holotype and UNSM 56304–56309, UNSM 56312, and UMMP 53019 (partial or whole mandibles with lower teeth); UNSM 56302, 56303, 56310, 56313, and UMMP 53025 (partial maxillae with upper teeth).

*Etymology*.—*trojectio*, Latin, crossing; *ansrum*, Latin, genitive plural of goose, meant to indicate the locality where the type was recovered.

*Diagnosis*.—Smallest known Tertiary species of *Perognathus*; P<sub>4</sub> three- or four-cusped and much smaller relative to M<sub>1</sub> than in other species.

*Description*.—The mandible of *P. trojectionansrum* is slender and does not differ from other species of *Perognathus*. The lower incisor is narrow with a convex anterior surface. The upper incisor is unknown.



Table 2.—Measurements of the dentition of *Perognathus trojectionansrum*.

UNSM no.	P <sup>4</sup>			M <sup>1</sup>			M <sup>2</sup>			M <sup>3</sup>			alveo- lar length
	A-P	tra	trp	A-P	tra	trp	A-P	tra	trp	A-P	tra	trp	
56302	0.93	0.53	1.06	0.72	0.99	1.02	—	—	—	—	—	—	—
56303	0.94	0.50	1.04	—	—	—	—	—	—	—	—	—	—
56310	—	—	—	0.76	0.95	0.87	—	—	—	—	—	—	—
56313	1.03	0.55	0.99	0.75	1.00	1.01	—	—	—	—	—	—	—

UNSM no.	P <sub>4</sub>			M <sub>1</sub>			M <sub>2</sub>			M <sub>3</sub>			alveo- lar length
	A-P	tra	trp	A-P	tra	trp	A-P	tra	trp	A-P	tra	trp	
56304	0.64	0.47	0.58	0.71	0.81	0.76	0.65	0.81	0.75	—	—	—	3.04
56305	0.66	0.56	0.75	—	—	—	—	—	—	—	—	—	—
56306	—	—	—	0.83	0.87	0.84	0.68	0.84	0.81	—	—	—	2.49
56307	0.63	0.47	0.58	—	—	—	—	—	—	—	—	—	—
56308	0.55	0.47	0.47	—	—	—	—	—	—	—	—	—	—
56309	0.57	0.47	0.61	0.73	0.79	0.82	—	—	—	—	—	—	—
56311	0.55	0.44	0.58	0.72	0.75	0.79	0.57	0.80	0.80	0.48	0.64	0.44	2.37
56312	0.67	0.39	0.62	—	—	—	—	—	—	—	—	—	2.86

UNSM no.	I <sub>1</sub>	
	A-P	width
56304	0.69	0.41
56307	0.77	0.38

Cheek teeth are low crowned and cuspsate when unworn or little worn. The teeth become lophate after moderate wear. P<sub>4</sub> is quite variable in pattern. In the holotype, the two cusps in the hypolophid (hypoconid and entoconid) are of equal size and widely separated. The metaconid and protostylid of the metalophid are subequal, transversely aligned and separated almost as much as the cusps of the hypolophid. A minute hypostylid is present on two specimens.

Most of the variation of P<sub>4</sub> is on the metalophid. The protostylid on P<sub>4</sub> of the two specimens is reduced and slightly posterior to the metaconid. P<sub>4</sub> in UNSM 56307 is quadricuspsate but differs from all other specimens in having an elevated metalophid. Two more specimens have single-cusped metalophids with the cusp centrally located on the lophid. In one of these, the three-cusped P<sub>4</sub> is roughly circular in outline with the three cusps placed peripherally on the tooth surrounding a central basin.

The size of P<sub>4</sub> is much reduced relative to M<sub>1</sub> and M<sub>2</sub>.

M<sub>1</sub> and M<sub>2</sub> are six-cusped and do not vary in morphology from any other species of *Perognathus*. The only known specimen of M<sub>3</sub> of *P. trojectionansrum* is moderately worn, so no details of cusp morphology can be accurately determined. The hypolophid appears bicuspsate, with the hypostylid absent.

The upper dentition of *P. trojectionansrum* is represented only by P<sup>4</sup> and M<sup>1</sup>. These teeth are also similar to all other species of the genus. P<sup>4</sup> has the basic four-cusped heteromyid pattern. M<sup>1</sup> consists of two transverse rows of three cusps divided by a central valley. Alveoli show that M<sup>3</sup> is much reduced in size.

*Discussion.*—*Perognathus trojectionansrum* is the smallest recorded species of *Perognathus*. James (1963) described *P. minutus* from the Cuyama Valley of California and stated that it was smaller than any

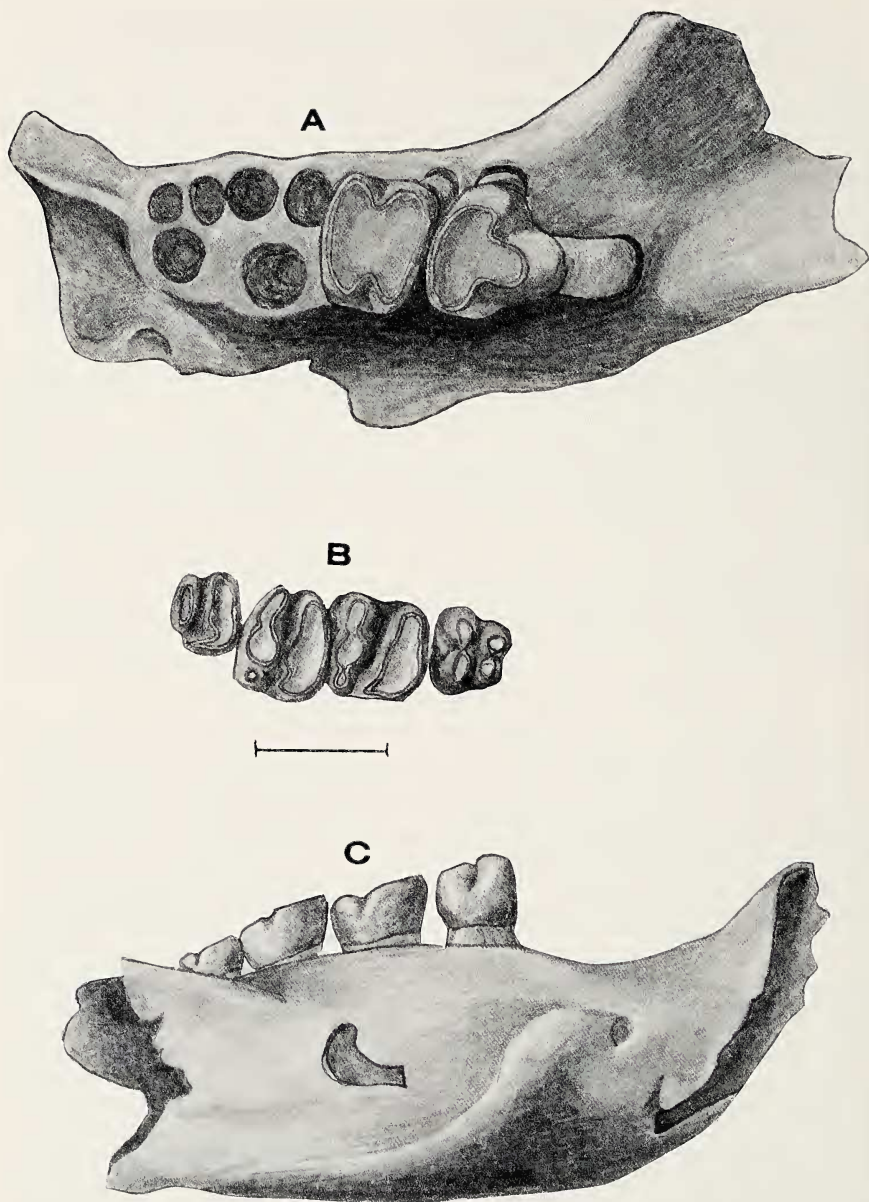


Fig. 3.—*Perognathus trojectionansrum*. A) UNSM 56313, RP<sup>4</sup>–M<sup>1</sup>. B) UNSM 56311, occlusal view, P<sub>4</sub>–M<sub>3</sub>. C) Lateral view of same. Scale = 1 mm.

fossil or Recent species of the genus. In all dimensions of the lower dentition, *P. trojectioansrum* is smaller than any recorded specimen of *P. minutus* (Lindsay, 1972). The upper dentition of *P. trojectioansrum*, however, is within the observed size range for *P. minutus*, though generally in the lower part of the range. It is possible that the upper teeth referred to *P. trojectioansrum* may be *P. minutus*, and only the lower dentitions are of the former. However, it seems highly improbable that one species would be represented by only upper and the other only lower teeth. There is no indication that either the lower or the upper dentitions assigned to *P. trojectioansrum* represent more than a single species.

The pattern of the molars in *Perognathus trojectioansrum* does not differ from that of any other species of the genus. The only tooth showing some variation from the basic *Perognathus* pattern is  $P_4$ , although the nature and form of the variation is not unique to heteromyid species.

Galbreath (1953) described a large sample of *Heliscomys* from the Oligocene of Colorado which showed much of the same variation in number and pattern of cusps on  $P_4$  as in *P. trojectioansrum*. Similar ranges of variation on this tooth have also been observed in Recent populations of *Perognathus* (Sutton, manuscript).

In proportions of teeth, *P. trojectioansrum* is quite similar to *Heliscomys*. Both forms are characterized by small size and  $P_4$  being disproportionately small with variable morphology.

### *Cupidinimus* Wood, 1935

*Perognathoides* Wood, 1935

*Peridiomys* (in part) Wood, 1935A.

*Cupidinomys nomen nudum* Shotwell and Russell, 1963.

*Prodipodomys*? (in part) Shotwell, 1967.

*Perognathus* (in part) Storer, 1970.

*Emended diagnosis*.—Generally small heteromyids; mesodont and lophate rooted teeth;  $M_1^1$  and  $M_2^2$  six-cusped;  $P^4$  with variable occurrences of accessory cuspules on the protoloph within species;  $I_1$  slender and rounded anteriorly; upper incisor asulcate;  $P_4$  with central union of lophids and variable occurrence of minor cusps on the meta-lophid and hypolophid; cingula distinct on molars.

*Range*.—Barstovian and Clarendonian (Miocene) of western North America.

*Type species*.—*Cupidinimus nebraskensis* Wood, 1935:118.

### *Cupidinimus nebraskensis* Wood, 1935

(Figs. 4, 5, 6 and Table 3)

*Emended diagnosis*.—Small size;  $P_4$  with variable occurrence of hypoconulid, anteroconid and protoconid;  $P^4$  with accessory cuspule on

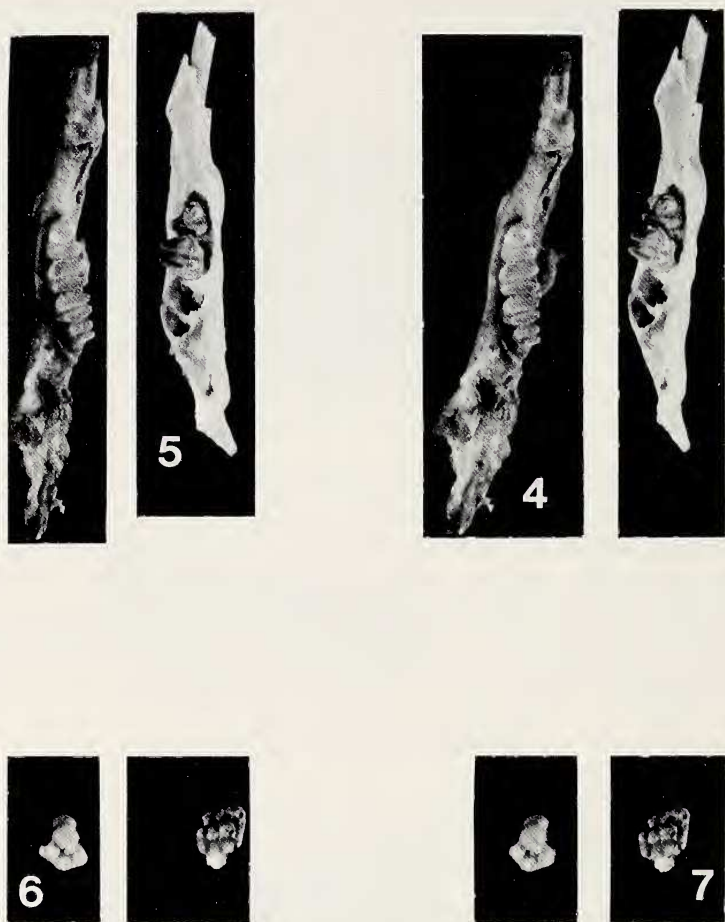


Fig. 4.—*Cupidininus nebraskensis*, stereoview, CM 10193 holotype,  $LP_4-M_3$ .  $\times 5.25$ .

Fig. 5.—*Cupidininus nebraskensis*, stereoview, UNSM 56127,  $RP_4-M_1$ .  $\times 5.25$ .

Fig. 6.—*Cupidininus nebraskensis*, stereoview, UNSM 56269,  $LP^4$ .  $\times 5.25$ .

Fig. 7.—*Perognathus trojectionansrum*, stereoview, UNSM 56310,  $RM^1$ .  $\times 5.25$ .

protoloph in some specimens;  $M_2^2$  and  $M_3^3$  reduced relative to  $M_1^1$ ; teeth mesodont; no hypostylid on  $P_4$

*Referred material*.—UNSM 56100, 56103, 56105–56113, 56115–56136, 56143–56227, 56299, 56357, 56360 (all lower teeth and mandible fragments), and UNSM 56101, 56102, 56104, 56114, 56137–56142, 56228–56298, 56361 (upper teeth and whole or partial maxillae).

*Description*.—Wood (1935) adequately described the molars and mandible of *C. nebraskensis*, based on skeletal material and dentitions consisting of one nearly complete



Table 3.—*Measurements (alveolar length) of the dentition of Cupidinus nebraskensis.*

Teeth	Measure- ments	N	M	SD	CV	OR	Paratype (CM 10170)	Holotype (CM 10193)
Maxillary tooththrow		9	3.93	0.24	6.11	3.53–4.21	3.83	
I <sup>1</sup>	A–P	1	0.92	—	—	—	—	
	width	1	0.60	—	—	—	—	
dP <sup>4</sup>	A–P	1	0.88	—	—	—	—	
	tra	1	0.77	—	—	—	—	
	trp	1	0.95	—	—	—	—	
P <sup>4</sup>	A–P	61	1.43	0.13	9.10	1.14–1.70	1.28	
	tra	61	0.70	0.07	10.00	0.55–0.85	0.68	
	trp	61	1.23	0.12	9.76	0.96–1.41	1.17	
M <sup>1</sup>	A–P	28	0.85	0.07	8.25	0.74–1.03	0.76	
	tra	28	1.15	0.11	9.56	0.96–1.50	1.05	
	trp	28	1.07	0.07	6.54	0.92–1.21	1.02	
M <sup>2</sup>	A–P	4	0.66	0.04	6.06	0.60–0.71	0.69	
	tra	4	0.96	0.07	7.29	0.92–1.06	0.96	
	trp	4	0.84	0.07	8.33	0.78–0.94	0.85	
M <sup>3</sup>	A–P	2	0.50	—	—	0.47–0.52	0.55	
	tra	2	0.64	—	—	0.62–0.65	0.69	
	trp	2	0.53	—	—	0.49–0.57	0.67	
Mandibular tooththrow		31	3.67	0.06	4.58	3.41–4.08		3.59
I <sub>1</sub>	A–P	28	0.89	0.06	7.28	0.78–1.03		0.88
	width	28	0.57	0.08	13.20	0.48–0.76		0.47
dP <sub>4</sub>	A–P	3	1.18	—	—	1.11–1.29		—
	tra	3	0.69	—	—	0.60–0.77		—
	trp	3	0.80	—	—	0.76–0.87		—
P <sub>4</sub>	A–P	88	1.00	0.08	8.07	0.78–1.18		0.95
	tra	88	0.72	0.07	9.59	0.59–0.91		0.74
	trp	88	0.90	0.08	8.56	0.75–1.11		0.90
M <sub>1</sub>	A–P	74	0.89	0.07	7.86	0.76–1.07		0.82
	tra	74	1.06	0.09	8.39	0.88–1.27		1.00
	trp	74	1.05	0.08	7.70	0.90–1.26		0.95
M <sub>2</sub>	A–P	14	0.76	0.06	8.33	0.66–0.85		0.67
	tra	14	1.01	0.09	8.86	0.88–1.21		0.95
	trp	14	0.95	0.07	7.62	0.85–1.11		0.89
M <sub>3</sub>	A–P	2	0.66	—	—	0.65–0.67		0.70
	tra	2	0.81	—	—	0.70–0.92		0.70
	trp	2	0.71	—	—	0.66–0.76		0.60

mandible with all teeth and a maxilla with P<sup>4</sup>–M<sup>3</sup>, two P<sup>4</sup>s, and two partial mandibles with dP<sub>4</sub> (and M<sub>1</sub> in one instance). The UNSM material referred to this species allows for a more complete description and a better understanding of the variability in morphology of the premolars.

According to Wood (1935),  $P_4$  of *C. nebraskensis* has a simple four-cusped pattern, with the hypolophid wider than the metalophid. The holotype (CM 10193), which contained the only known  $P_4$ , does have a minor anteroconid in the center of the metalophid. Due to the state of wear, this cuspule is preserved as an anterior bend in the enamel surrounding the anterior wear facet of the tooth. This anterior extension gives the metalophid a trilobed appearance with the central lobe being the smallest.

In the UNSM sample there is a great deal of variation in the morphology of  $P_4$ . On approximately 80% of the specimens a minute anteroconid occurs on the metalophid. The anteroconid is usually central, but can appear on the internal slope of either the metaconid or protostylid.

A protoconid is present on about half of the specimens. It is smaller than either of the other two metalophid cusps and slightly posterior to them. The posterior slope of the protoconid extends posteriorly, in many cases, to form a minor ridge which runs antero-posteriorly. This minor ridge is similar to that reported on  $P_4$  of "*Perognathus*" *saskatchewanensis* (Storer, 1970, 1975).

The hypolophid, as noted by Wood (1935), is broad and composed of two major widely spaced cusps. Some specimens have a central hypoconulid. It is generally a swelling between the major cusps and varies in size from minute to subequal with the other hypolophid cusps.

Presence of any or all of these three additional cusps (anteroconid, protoconid, hypoconulid) on a  $P_4$  is variable and appears totally random.

There is no hypostylid on the metaloph of  $P_4$  of *C. nebraskensis*. On three of the 88 specimens, there is a minute anterior projection from the hypoconid that may be homologous to a hypostylid, but does not develop into a cusp.

The protoloph of  $P^4$  has an accessory cuspule in 15% of the sample. This cuspule can occur either buccal or lingual to the protocone and either at the base or near the tip of the latter.

The posterior portion of the mandible of the holotype is damaged and little can be said of the morphology of the bone in this area. Wood (1935:128) reconstructs the probable shape of the coronoid, condyle, and angle of the mandible on the holotype. Specimens in the present sample show that the mandibular condyle is perhaps a bit higher than in Wood's figure, but otherwise the restoration is quite accurate. The angle of the mandible is inflected slightly. The medial foramen on the ascending ramus is about halfway between  $M_3$  and the tip of the condyle. The coronoid process is short and slender, and deflects externally away from the ramus.

The bulbous lateral expansion on the ascending ramus marking the pulp cavity of the incisor is small and nearly circular. It rises only slightly above the wall of the ramus.

*Discussion.*—In Wood's (1935) review of the Heteromyidae two new genera, *Perognathoides* and *Cupidinimus* were described. Both genera were described as having asulcate upper incisors, progressively hypsodont rooted molars, and perognathine tooth pattern ( $P_4$  with union of lophs central and H-pattern of lophid union on lower molars). *Cupidinimus* was described as having progressive deciduous premolars, calcaneal-navicular articulation in the tarsus, and a subricochetal mode of locomotion. None of these traits was referred to in his description of *Perognathoides*. *Perognathoides* was characterized as having a lingual and buccal cuspule on the protoloph of  $P^4$ , a character considered unique to this genus.

Wood (1935) failed to compare these two forms directly, although

the great similarity of these two genera was recognized by a number of later authors (Wilson, 1939; Downs, 1956; Lindsay, 1972). The criteria that were used to separate these two genera appear inadequate to warrant generic separation.

The premolars of *Cupidinimus nebraskensis* are more complex than initially recognized by Wood (1935). The morphology of  $P_4^4$  is variable and consists of characters that have been associated with other genera of heteromyids (notably *Perognathoides*, Wood, 1935).

The variable presence of a protoconid on  $P_4$ , small size and relative reduction of  $M_2^2$  and  $M_3^3$  make *C. nebraskensis* distinct from similar mesodont species of heteromyids. Lindsay (1972) referred a number of specimens from the Barstow Formation of California to *C. nebraskensis*. However, the Barstow material lacks any of the accessory cusps on  $P_4^4$ , is smaller in size, possesses a hypostylid on  $P_4$  (not found in the Nebraska sample), and does not have reduced  $M_2^2$  or  $M_3^3$ . This California species is clearly not referable to *C. nebraskensis*, and should be designated as a new species of *Cupidinimus*.

Although Wood (1935) diagnosed the genus as having progressively hypsodont teeth, *C. nebraskensis* was defined as being low crowned. Teeth of *C. nebraskensis* are evidently mesodont in height and equal to or nearly equal to that of species of *Perognathoides*.

Wood (1935) inferred the mode of locomotion of *Cupidinimus* from the proportions of limb bones and the structure of the tarsus. At the time, no postcranials were known for *Perognathoides*. It was also impossible to compare the deciduous premolars of *Cupidinimus* to *Perognathoides*, for which the deciduous premolars were unknown. Hence, the only character available for comparison at the time of description of the two genera was the presence of accessory cuspsules on the protoloph of  $P^4$ . Although this trait was cited as diagnostic for *Perognathoides*, there was evidence of accessory cuspsules on only one of the two species assigned to the genus. The only known  $P^4$  of *P. tertius* (later referred to *P. halli*, Wood, 1936a) is well worn and shows no evidence of a distinct cuspsule on either side of the protocone. Wood (1935) inferred the presence of two accessory cuspsules from the slight transverse elongation of the protoloph. Later, Wood (1937) described a species of *Perognathoides*, *P. cuyamensis*, which possessed only a single cuspsule on the protoloph of  $P^4$ . James (1963) found this to be a variable trait on *Perognathus* and questioned its diagnostic value for *Perognathoides*.

Lindsay (1972), studying the first extensive collection of *Perognathoides*, found that accessory cuspsules on  $P^4$  occurred on half of the sample of 50 specimens. The variability of this character in *Cupidinimus nebraskensis*, *Perognathoides halli* (Lindsay, 1972), *Perognathus*



*furlongi* (James, 1963), and "*Diprionomys*" *agrarius* (see below) indicates that this character does not separate *Cupidinimus* from *Perognathoides*.

Wood (1935) thoroughly described the postcranial skeleton of *C. nebraskensis*. It most closely resembles that of *Perognathus* with a number of characters tending toward specializations for ricochetal locomotion seen in Recent *Dipodomys*. The only postcranial elements reported for *Perognathoides* are calcanea from California assigned to *P. cuyamensis* (Wood, 1937). They are described as being more slender than the calcaneum of *Perognathus*, a character cited for Recent ricochetal forms but not specifically noted for the calcaneum of *Cupidinimus* (Wood, 1935).

No calcaneum or cuboid is present among the postcranial bones of the holotype of *C. nebraskensis* (CM 10193) though measurements for one are listed in Wood (1935, table III). In his reconstruction of the pes of *C. nebraskensis*, Wood (1935:139) figures a calcaneum restored from another specimen, not in the Carnegie Museum of Natural History collections. The navicular on the holotype is badly abraded with cancellous bone exposed on one surface. No articular surfaces are evident on the lateral side of the navicular making it impossible to determine the nature of the calcaneal contact with other tarsal bones. Korth (1979) assigned several isolated calcanea and astragali to *C. nebraskensis* (= *Cupidinimus* sp. B). When these elements are articulated, the distal margin of the calcaneum does not extend beyond that of the astragalus. One calcaneum can be articulated with the tarsal elements of the holotype, and does not extend distal to the astragalus, or articulate with the navicular.

Wood (1935) used presence of a calcaneum-navicular contact to diagnose *Cupidinimus* and as the basis for assigning it to the Dipodomysinae (although it was also cited as occurring in *Paramys*). Because this character cannot now be verified, it seems advisable to eliminate it from the diagnosis of the genus.

Thus, based on dental morphologies, *Cupidinimus* is inseparable from *Perognathoides*. The synonymy of these genera poses a minor nomenclatural problem because both were named in the same paper. More species have been assigned to *Perognathoides* than *Cupidinimus*. However, the genoholotype of *Cupidinimus* (*C. nebraskensis*) is an excellent specimen consisting of a partial skull, nearly complete mandible with all teeth present and little worn, and a great deal of the postcranial skeleton. The genoholotype of *Perognathoides* (*P. quartus*) is a partial skull with heavily worn incomplete dentition, and a single referred specimen, a mandible, also has badly worn dentition. For comparison, it is much more advantageous to refer these species



to *Cupidinimus* rather than *Perognathoides*. An extensive collection of *C. nebraskensis* is available for comparison, whereas *P. quartus* is known from only two specimens. Thus, *Cupidinimus* seems a better choice for the generic assignment. A formal revision is presently impractical because many species have been diagnosed on poorly preserved material and known from only limited hypodigms. Species that are well represented show a great deal of variability and render the original diagnoses inapplicable. Due to this wide variability and limited number of specimens, systematic revisions are not dealt with specifically here, pending a formal revision of the species of the genus.

Because the genoholotype of *Perognathoides* is in such poor condition, it could be argued that it is generically indeterminate. Thus, the referral of all species assigned to *Perognathoides* with known occlusal pattern of the teeth to *Cupidinimus* would not mean the synonymy of these two genera. However, in all observable characters *P. quartus* is congeneric with *Cupidinimus*.

All species previously assigned to *Perognathoides* should be referred to *Cupidinimus* (*P. quartus* [Hall, 1930]; *P. tertius* [Hall, 1930]; *P. halli* Wood, 1936a; *P. cuyamensis* Wood, 1937; *P. cf. tertius* Wilson, 1939; *P. madisonensis* Dorr, 1956; *P. continentalis*, *nomen nudum* Reeder, 1958; *P. cf. P. cuyamensis* Klingener, 1968; *P. kleinfelderi* Storer, 1970; *P. eurekensis* Lindsay, 1972). A thorough study of these species may indicate that specific systematic revisions may be necessary. Lindsay (1972) suggested some synonymies but only dealt with a few species of *Perognathoides* and not the entire genus along with the species of *Cupidinimus*.

In addition to the species of *Perognathoides*, a number of other forms are probably also referable to *Cupidinimus*. Storer (1970) described *Perognathus saskatchewanensis* from the Wood Mountain Formation of Saskatchewan. This species was diagnosed by possession of an anteroconid on  $P_4$  and presence of a central longitudinal ridge on the same tooth, features considered unique to species of *Perognathus*. Storer failed to discuss crown height of this species, or to provide figures depicting this dimension (also see Storer, 1975). When specimens of "*Perognathus*" *saskatchewanensis* are compared with other species of *Perognathus* and *Cupidinimus*, it is apparent that "*P.*" *saskatchewanensis* is mesodont as is *Cupidinimus*, much higher crowned than *Perognathus*. The occurrence of an anteroconid on most specimens of  $P_4$  of "*P.*" *saskatchewanensis* agrees with *C. nebraskensis* and other species referred here to the latter genus (Lindsay, 1972; Sutton, manuscript).

*Cupidinimus* sp. from the Mission local fauna (Clarendonian) of South Dakota (Green, 1971), *Prodipodomys? mascalensis* from the

Quartz Basin (Barstovian) of Oregon (Shotwell, 1967), and *Cupidinomyx* sp. from the Juntura Basin (Clarendonian) of Oregon are probably also referable to *Cupidinimus*.

The distinction between some of the species referred here to *Cupidinimus* is quite subtle and often is based only on mean size of an extensive sample as in *C. halli* and *C. madisonensis* (Sutton, manuscript). These discrete differences are observed only when large samples of the species are known. Because of this, difficulties arise in the allocation of specimens to any species of *Cupidinimus* unless an adequate sample of fossils is known. More extensive collections of known species discussed above may well suggest systematic revisions of the species of *Cupidinimus*.

***"Diprionomys" agrarius* Wood, 1935**  
(Figs. 8, 9 and Table 4)

*Referred material.*—UNSM 56353–56356 (P<sup>4</sup>s), UNSM 56349 (RP<sub>4</sub>), UNSM 56350 (LM<sub>1</sub> or M<sub>2</sub>), UNSM 56351 (LM<sub>3</sub>), UNSM 56352 (edentulous mandible), UNSM 56358 (LdP<sup>4</sup>) and UNSM 56359 (LdP<sub>4</sub>).

*Description.*—A left edentulous mandible is referable to this species based on the comparable size of known teeth and the presence of alveolae for roots on all teeth. The mandible is broken away anterior to the alveolus for P<sub>4</sub>. The posterior part of the mandible is nearly complete. The ramus is quite deep and virutally identical to that of "*Diprionomys*" *agrarius* (Wood, 1935:180, 184).

All cheek teeth are low crowned. The crown height is perhaps slightly higher than in *Perognathus*, but clearly lower than in mesodont heteromyids like *Cupidinimus*. A single P<sub>4</sub> is present in the collection. It is basically four-cusped. The hypolophid has a distinct hypoconid and entoconid with no other cuspules. The metaconid shows moderate wear and is reduced to a large circular facet, which extends labially and posteriorly to another nearly circular facet in the center of the tooth. Posteriorly, this facet unites with the hypoconid by means of a narrow connection. A smaller protostylid is distinct from the metaconid facet and is unworn.

The lower molars referred to this species differ from the holotype of "*D.*" *agrarius* only in their slightly larger size.

P<sub>4</sub> has a simple pattern. The metaloph consists of three distinct cusps, the centrally placed hypocone being the largest. The metacone and entostyle are displaced slightly anterior to the hypocone giving the metaloph a posteriorly convex appearance. The protoloph contains a single protocone. On one specimen (UNSM 56356) there is a small cuspule just labial to the apex of the protocone.

DP<sub>4</sub> is lower crowned than P<sub>4</sub> and slightly more transverse anteriorly. It is composed of two main transverse lophs, each with two cusps. A third, anterior loph composed of a crescentic anterocone is connected to the posterior transverse loph via a strong lingual cingulum. The transverse valley between the main lophs is shallow. The anterocone is united with the central transverse loph labially.

*Discussion.*—In the morphology of the molars and mandible, the UNSM specimens are nearly identical with "*D.*" *agrarius*, known from the Cap Rock Member of the Ash Hollow Formation in Nebraska (Wood, 1935) and the Norden Bridge local fauna (Klingener, 1968) of the Valentine Formation. Morphologically, P<sub>4</sub> from locality Kx 110 is



Fig. 8.—“*Diprionomys*” *agrarius*, stereoview, UNSM 56356, LP<sup>4</sup>.  $\times 5.25$ .

Fig. 9.—“*Diprionomys*” *agrarius*, stereoview, UNSM 56349, RP<sub>4</sub>.  $\times 5.25$ .

quite different from  $P_4$  in the holotype of “*D.*” *agrarius*, which has a distinct anteroconid, and the metaconid and protostylid separated by a deep longitudinal valley. The only  $P_4$  assigned here to “*Diprionomys*” *agrarius* shows a remnant of what may have been a protoconid displaced posterior to the other metalophid cusps. The union of the lophs is, however, not central and a minor central depression is present.

Klingener (1968) described five  $P_4$ s of “*D.*” *agrarius* from the Norden Bridge local fauna. He noted the differing degree of complexity of the metalophid of  $P_4$  and established a size range for this tooth that is large enough to include the Kx 110 material.

Table 4.—Measurements of the dentition of "*Diprionomys*" *agrarius*.

Teeth	UNSM no.	A-P	tra	trp
dP <sup>4</sup>				
	56358	1.66	1.19	1.59
P <sup>4</sup>				
	56353	1.75	0.85	1.62
	56354	—	0.90	1.78
	56355	1.63	0.90	1.83
	56356	1.84	0.96	1.87
dP <sub>4</sub>				
	56359	2.04	0.97	1.35
P <sub>4</sub>				
	56349	1.44	1.12	1.36
M <sub>1</sub> or M <sub>2</sub>				
	56350	1.51	1.82	1.77
M <sub>3</sub>				
	56315	1.35	1.53	1.50

The two lower molars assigned to "*D.*" *agrarius* are slightly larger than those of the holotype. The differences in size, however, are no greater than those recorded by Klingener (1968) for the premolar. The hypostylid on M<sub>3</sub> of the UNSM material is slightly larger than that of the holotype but not significantly so. No other differences in morphology exist in the molars.

The variability in the metalophid of P<sub>4</sub> is also reflected by the occasional occurrence of an accessory cuspule near the apex of the protocone on the protoloph of P<sup>4</sup>, a character also noted in *D. cf. parvus* from Nevada (Clark et al., 1964).

"*Diprionomys*" *agrarius* was initially described by Wood (1935) and assigned to the same genus *Diprionomys parvus* (Kellogg, 1910) from the Clarendonian of Nevada. "*D.*" *agrarius* differs most markedly from *D. parvus* in size and crown height. The molars of *D. parvus* are quite high crowned as implied by the straight lateral walls of the teeth. "*D.*" *agrarius*, however, is very low crowned. The crowns of the latter are quite similar in height to those of *Peridiomys*.

Because of the difference in crown height between "*D.*" *agrarius* and *D. parvus*, Reeder (1958) included "*D.*" *agrarius* in a new genus (*Halticosomys*, *nomen nudum*). Two isolated teeth from the Fish Lake Valley fauna of Nevada were identified as *D. cf. parvus*, based on size. From the figures (Clark et al., 1964), these specimens appear lower crowned than the holotype of *D. parvus* (Kellogg, 1910) and the



P<sup>4</sup> possesses an accessory cuspule as in "*D.*" *agrarius*. "*D.*" cf. *parvus*, therefore, may represent a distinct species assignable to a new genus which would also include "*D.*" *agrarius*. At present, none of these species (*D. parvus*, "*D.*" *agrarius*, "*D.*" cf. *parvus*) are well known. Recognition of a new genus separate from *Diprionomys* to include "*D.*" *agrarius* and "*D.*" cf. *parvus* should await a formal review of the entire Heteromyidae. For convenience, "*D.*" *agrarius* is retained in the genus with question until it is better known and a more detailed study is made.

### Family Geomyidae

#### Subfamily uncertain

#### *Lignimus* cf. *L. hibbardi* Storer, 1973

(Figs. 10, 11, 12 and Table 5)

*Referred material.*—UNSM 56316–56326 (P<sub>4</sub>s), UNSM 56327–56337 (P<sub>4</sub>s), UNSM 56339, 56340, 56346 (lower molars), UNSM 56338, 56341–56345, 56347, 56348 (upper molars) and UNSM 56315 (an edentulous mandible).

*Description.*—A left mandible lacking cheek teeth is here assigned to *Lignimus*. This allocation seems certain because the size is comparable with the isolated teeth and there is no indication of sockets for any roots in the molar alveoli.

The angle and a portion of the lateral wall of the mandible is broken away. The diastema is shallow and relatively short. The mental foramen is situated below the center of the diastema and halfway between the ventral and dorsal margins of the bone. The ridge marking the attachment of the masseter muscle terminates just dorsal and posterior to the mental foramen. It runs posteriorly, directed toward the ventral margin of the jaw at the level of M<sub>3</sub>. The posterior extent of this ridge is uncertain because the bone is broken in this area.

The alveolar margin forms a straight anteroposterior ridge. The ascending ramus blocks only M<sub>3</sub> in lateral view. It is broad and rises well above the molars. The condyle is about as high as the coronoid, which is relatively low and blunt. There is a distinct basin area just below the condyle that extends anteriorly to the coronoid process and ventrally to the lateral expansion of the jaw marking the pulp cavity of the incisor. Medially, there is a depression lateral to M<sub>3</sub> extending onto the ascending ramus to just below the coronoid. The medial foramen of the ascending ramus is nearly midway between M<sub>3</sub> and the condyle, but slightly closer to the latter.

The enamel of the lower incisor is thin. The anterior margin of this tooth is flattened and broad. In cross section, the tooth gradually tapers posteriorly.

The cheek teeth are hypsodont. All premolars and a single specimen of M<sup>1</sup> are rooted. All other molars lack roots. The lower premolars are vitally identical with the holotype of *L. hibbardi*, possessing one or two anterostylids, with lateral and lingual dentine tracts extending to ¼ or ⅓ the height of the crown from the base of the enamel.

The lower molars are recurved and rootless. Dentine tracts extend dorsally to about half the height of the crown. The occlusal pattern is that described for *L. hibbardi* (Storer, 1973). The cusps rapidly wear into two straight transverse lophs that eventually unite centrally in an H-Pattern. The protoconids are not as distinctly isolated as in *L. montis*. P<sup>4</sup> has four cusps. The protoloph consists of the protocone that, in unworn specimens, is ovoid. The protocone wears to a shortened transverse loph. The metaloph of P<sup>4</sup> is simple. The entostyle, smallest of the three cusps, connects to the hypocone by a cingulum that curves forward from the latter. The entostyle is positioned anteriorly about halfway between the apices of the hypocone and protocone. The metaloph wears to a J-pattern, with the entostyle as the hook of the J.

Table 5.—*Measurements of the dentition of Lignimus cf. L. hibbardi.*

Teeth	UNSM no	A-P	tra	trp
P <sup>4</sup>	56327	1.58	1.06	1.88
	56328	1.75	1.08	1.93
	56329	1.71	1.17	1.88
	56330	1.64	1.00	1.79
	56331	1.46	0.86	1.73
	56332	1.71	1.20	1.83
	56333	1.55	1.10	1.86
	56334	1.70	1.27	1.91
	56335	1.72	1.12	1.87
	56336	1.56	1.06	1.73
	56337	1.47	0.92	1.78
M <sup>1</sup>	56338	1.16	1.87	1.72
	56344	1.01	1.68	1.56
	56345	1.18	1.71	1.59
M <sup>2</sup>	56341	1.08	1.52	1.47
	56343	1.06	1.52	1.37
	56348	—	1.55	1.46
M <sup>3</sup>	56342	1.10	1.41	1.25
	56347	0.93	1.47	1.43
I <sub>1</sub>	56315	1.42	1.18 (width)	
P <sub>4</sub>	56316	1.81	1.13	1.59
	56317	1.85	1.34	1.54
	56318	1.81	1.35	1.62
	56319	1.82	1.35	1.66
	56320	1.92	1.47	1.72
	56321	1.89	1.30	1.64
	56322	1.89	1.32	1.48
	56323	2.04	1.27	1.58
	56324	1.98	1.52	1.66
	56325	1.90	1.36	1.66
	56326	1.60	1.18	1.61
M <sub>1</sub>	56346	1.19	1.69	1.58
M <sub>2</sub>	56340	1.11	1.58	1.51
M <sub>3</sub>	56339	1.06	1.39	1.39

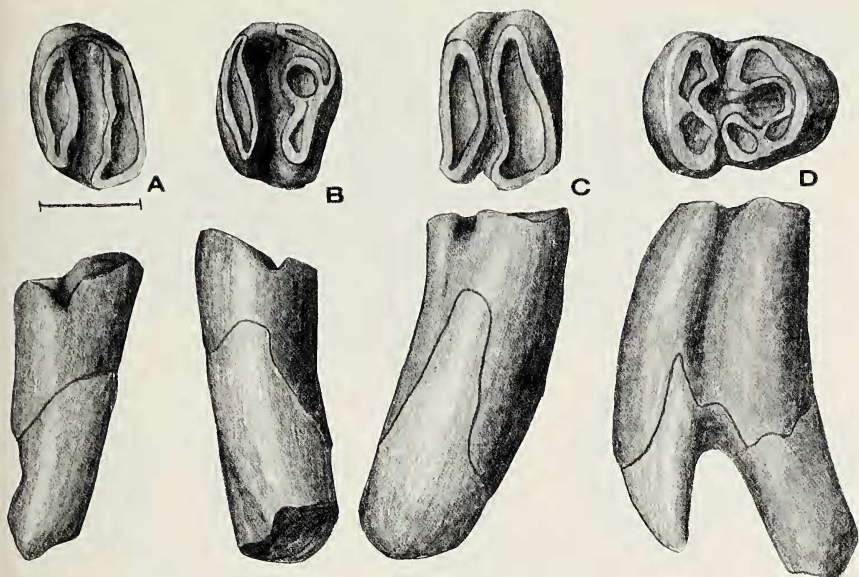


Fig. 10.—Occlusal and lateral view of lower cheek teeth of *Lignimus* cf. *L. hibbardi*. A) UNSM 56339, RM<sub>3</sub>. B) UNSM 56340, LM<sub>2</sub>. C) UNSM 56346, RM<sub>1</sub>. D) UNSM 56322, RP<sub>4</sub>. Scale = 1 mm.

The upper molars are also recurved. The extent of the lateral dentine tracts is about half the height of the crown, and perhaps slightly more on M<sup>3</sup>. All upper molars share the same occlusal pattern as in *L. hibbardi*, and decrease in size from M<sup>1</sup> to M<sup>3</sup>. The molars have two distinct transverse lophs. The lophs are joined lingually by an internal cingulum. There is evidence of roots on only one specimen of M<sup>1</sup>, where they are short stubs equal to less than 10% of the total height of the tooth. P<sup>4</sup> has three roots. The anterior root is strong and the posterior roots are weak.

*Discussion.*—Storer (1973) identified a number of specimens from the Norden Bridge local fauna and the Crookston Bridge Member of the Valentine Formation (Cherry County, Nebraska) as *Lignimus* sp. He noted similarities between these specimens and *L. hibbardi* from Kansas. The only difference cited between *Lignimus* sp. and *L. hibbardi* was the relative extent of the dentine tracts on the molars, which reached about  $\frac{2}{3}$  of the height of the crown in *L. hibbardi* and only  $\frac{1}{2}$  the height in *Lignimus* sp.

Both of these species differ from *L. montis*, the type species, in occlusal pattern of the molars and premolars, the presence of dentine tracts on the lateral walls of the cheek teeth, and lack of roots on the molars. The lower molars of *L. hibbardi* and the Nebraska species do not form the distinct X-pattern of *L. montis*. In the former, the rows

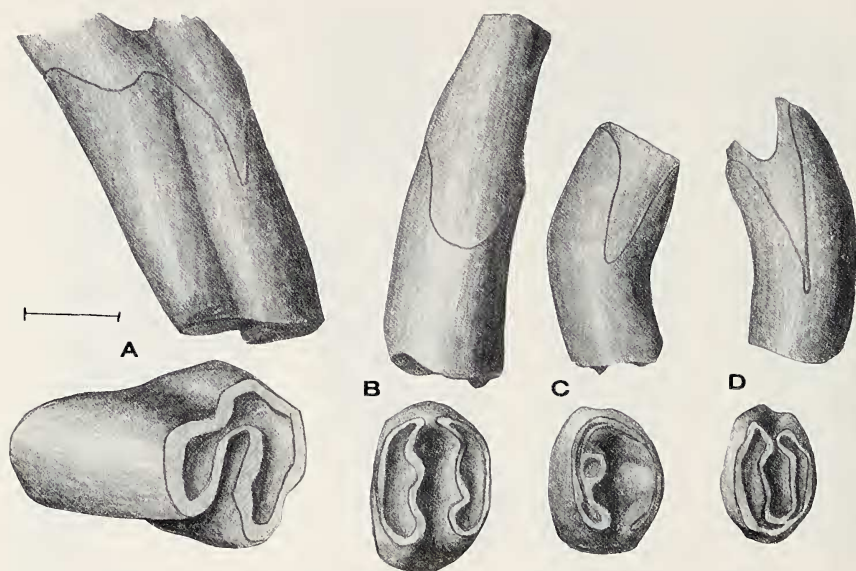


Fig. 11.—Medial and occlusal views of upper cheek teeth of *Lignimus* cf. *L. hibbardi*. A) UNSM 56329, RP<sup>4</sup>. B) UNSM 56345, RM<sup>1</sup>. C) UNSM 56343, RM<sup>2</sup>. D) UNSM 56342, LM<sup>3</sup>. Scale = 1 mm.

of cusps are more nearly parallel and wear as two separate transverse lophs, finally uniting centrally in a pattern more similar to the H-pattern of heteromyids (see Wood, 1935). Also, in *L. hibbardi* and the Nebraska species, the anterior cingulum is more closely appressed to the protoconid than in *L. montis* and does not form the anterobuccal enamel lake when worn as in the latter.

The lower premolars of the Kansas and Nebraska species are characterized by a distinct central trigonid basin surrounded by multiple cusps. The major cusps (protostylid and metaconid) are widely separated and connected to an anteriorly curving loph composed of one or two smaller cusps. *L. montis* has no such basin. The metalophid consists of two major cusps that are only separated by a narrow valley, and one or two additional smaller cusps, not arranged in the same way as in *L. hibbardi*.

P<sup>4</sup> of *L. montis* has a large circular protocone and an additional anterocone in some specimens. No known specimens of P<sup>4</sup> of *Lignimus* from Kansas or Nebraska have an anterocone. The protoloph on P<sup>4</sup> of the latter is flattened anteriorly and is a transverse loph when worn. On unworn specimens this cusp is simple and ovoid in shape.

In *L. montis* all teeth are rooted and there is no interruption in



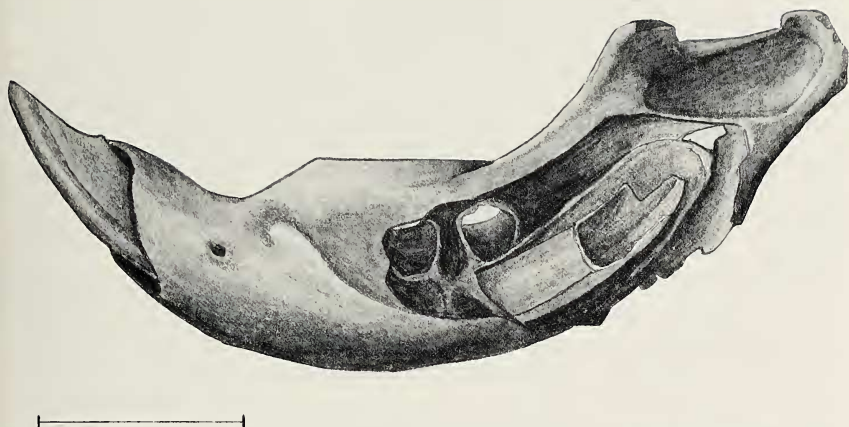


Fig. 12.—Lateral view of left mandible of *Lignimus* cf. *L. hibbardi*, UNSM 56315. Scale = 5 mm.

enamel on any side of the tooth. *L. hibbardi* and *Lignimus* cf. *L. hibbardi* exhibit some degree of enamel failure on the lateral and lingual sides of the teeth, and the molars are rootless. The protocone on the upper molars of *L. montis* is large and somewhat isolated (Storer, 1970). The upper molars of the Kansas and Nebraska species have protocones which are subequal with the other three cusps of the teeth, and the depression separating the protocone from the cingulum is quite shallow and any trace of an enamel lake is rapidly eliminated.

The differences between the Kansas-Nebraska *Lignimus* and *L. montis* may be sufficient to warrant generic separation. However, these species are all poorly represented, known from isolated teeth only. Establishment of a new genus, if necessary, for the Kansas-Nebraska material should await recovery of more extensive collections and more complete material of these taxa.

Storer (1970, 1973, 1975) referred *Lignimus* to the Entoptychinae, based on the similarities of the cheek teeth with *Gregorymys*. Many of the similarities between *L. montis* and *Gregorymys*, however, are not present in the Kansas and Nebraska species. This indicates that either the species referred to *Lignimus* represent more than one genus or that the type species is unique and may be convergent with entoptychines.

The mandible here referred to *Lignimus* cf. *L. hibbardi* differs greatly from those of entoptychines (see Rensberger, 1971). It most closely resembles mandibles of more primitive pleurolicines (see Rensberger, 1974), though this similarity may only be a reflection of the primitive character of the mandible.

The cheek teeth of *L. hibbardi* and *L. cf. L. hibbardi* are quite similar to *Pliosacomys* (Wilson, 1936).

The Kansas and Nebraska forms of *Lignimus* are intermediate between *Pliosacomys* and *Parapliosacomys* in development of hypsodonty and completeness of enamel failure on the molars, and have a crown pattern similar to these forms. The Unique "X" pattern on the molars of *L. montis* is also present on the molars of *Dikkomys* (Wood, 1936b; Black, 1961) and may indicate a close relationship of these two forms.

Storer (1973) suggests that a specimen from the Clarendonian Avawatz fauna from California referred to "dipodomyine n. gen. and sp." by Wilson (1939) is actually *Lignimus*. However, from the figures available, the outline of  $P_4$  of the California species is clearly distinct from that of *Lignimus*. Also, the increased crown height and completeness of the enamel failure on the teeth of the Avawatz form are unequaled in any species of *Lignimus*.

#### SUMMARY

The geomyoids from Annie's Geese Cross locality are of little help in solving the "Valentinian" age problem. Two of the heteromyids, *Cupidinimus nebraskensis* and *Perognathus trojectionansrum*, are restricted to the Crookston Bridge Member of the Valentine Formation. "*Diprionomys*" *agrarius* is known from both the Clarendonian Cap Rock Member of the Ash Hollow Formation and the Barstovian Crookston Bridge Member of the Valentine Formation in Nebraska (Wood, 1935; Klingener, 1968) and from the Wood Mountain Formation (Barstovian) of Canada. *Perognathus furlongi* is known throughout the Barstow Formation of California. *Lignimus*, outside of Nebraska, is known from the Barstovian Wood Mountain fauna (Storer, 1975) and Clarendonian Ogallala Formation of Kansas (Storer, 1973).

More than these five species must be considered before a conclusion can be reached as to the age of the lower Valentine Formation.

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#### LITERATURE CITED

- BLACK, C. C. 1961. Rodents and lagomorphs from the Miocene Fort Logan and Deep River Formations of Montana. *Postilla*, 48:1-20.
- CLARK, J. B., M. R. DAWSON, AND A. E. WOOD. 1964. Fossil mammals from the Lower Pliocene of Fish Lake Valley, Nevada. *Bull. Mus. Comp. Zool.*, 131:27-63.

- DORR, J. A. 1956. Anceney local mammal fauna, latest Miocene, Madison Valley Formation, Montana. *J. Paleontol.*, 30:62–74.
- DOWNS, T. 1956. The Mascall fauna from the Miocene of Oregon. *Univ. California Publ., Geol. Sci.*, 31:199–354.
- GALBREATH, E. C. 1953. A contribution to the Tertiary geology and paleontology of northeastern Colorado. *Univ. Kansas Paleontol. Contrib., Vert.*, 4:1–120.
- GAZIN, C. L. 1930. A Tertiary vertebrate fauna from the upper Cuyama drainage basin, California. *Carnegie Inst. Washington, Publ.*, 404:55–76.
- GREEN, M. 1971. Additions to the Mission vertebrate fauna, Lower Pliocene of South Dakota. *J. Paleontol.*, 45:486–490.
- HALL, E. R. 1930. Rodents and lagomorphs from the later Tertiary of Fish Lake Valley, Nevada. *Univ. California Publ., Geol. Sci.*, 19:295–311.
- JAMES, G. T. 1963. Paleontology and nonmarine stratigraphy of the Cuyama Valley badlands, California. Part 1. Geology, faunal interpretations, and systematic descriptions of Chiroptera, Insectivora, and Rodentia. *Univ. California Publ., Geol. Sci.*, 45:1–154.
- KELLOGG, L. 1910. Rodent fauna of the late Tertiary beds at Virgin Valley and Thousand Creek, Nevada. *Univ. California Publ., Geol. Sci.*, 5:421–437.
- KLINGENER, D. 1968. Rodents of the Mio-Pliocene Norden Bridge local fauna, Nebraska. *Amer. Midland Nat.*, 80:65–74.
- KORTH, W. W. 1979. Taphonomy of microvertebrate fossil assemblages. *Ann. Carnegie Mus.*, in press.
- LINDSAY, E. H. 1972. Small mammal fossils from the Barstow Formation, California. *Univ. California Publ., Geol. Sci.*, 93:1–104.
- REEDER, W. G. 1958. A review of Tertiary rodents of the family Heteromyidae. *Diss. Abstr.*, 18:1548.
- RENSBERGER, J. M. 1971. Entoptychine pocket gophers (Mammalia, Geomyoidea) of the early Miocene John Day Formation, Oregon. *Univ. California Publ., Geol. Sci.*, 90:1–209.
- . 1974. Pleurolicine rodents (Geomyoidea) of the John Day Formation, Oregon, and their relationships to taxa from the early and middle Miocene, South Dakota. *Univ. California Publ., Geol. Sci.*, 102:1–95.
- SCHULTZ, C. B., M. R. SCHULTZ, AND L. D. MARTIN. 1970. A new tribe of saber-toothed cats (Barbourafelini) from the Pliocene of North America. *Bull. Univ. Nebraska State Mus.*, 9:1–31.
- SHOTWELL, J. A. 1967. Late Tertiary geomyoid rodents of Oregon. *Univ. Oregon Mus. Nat. Hist. Bull.*, 9:1–51.
- SHOTWELL, J. A., AND D. E. RUSSELL. 1963. Mammalian fauna of the Upper Juntura Formation, the Black Butte local fauna. Pp. 42–76, in *The Juntura Basin: studies in earth history and paleoecology* (J. A. Shotwell et al.), *Trans. Amer. Phil. Soc.*, 53:1–77.
- SKINNER, M. F., S. M. SKINNER, AND R. J. GOORIS. 1968. Cenozoic rocks and faunas of Turtle Butte, south-central South Dakota. *Bull. Amer. Mus. Nat. Hist.*, 138:379–436.
- STORER, J. E. 1970. New rodents and lagomorphs from the Upper Miocene Wood Mountain Formation of southern Saskatchewan. *Canadian J. Earth Sci.*, 7:1125–1129.
- . 1973. The entoptychine geomyid *Lignimus* (Mammalia: Rodentia) from Kansas and Nebraska. *Canadian J. Earth Sci.*, 10:72–83.
- . 1975. Tertiary mammals of Saskatchewan. Part III. The Miocene fauna. *Life Sci. Contrib., Royal Ontario Mus.*, 103:1–134.
- SUTTON, J. F. 1977. Mammals of the Anceney local fauna (late Miocene) of Montana. Unpublished Ph.D. dissert., University Microfilms, Ann Arbor.

- VOORHIES, M. R. 1971. Paleoclimatic significance of crocodilian remains from the Ogallala Group (Upper Tertiary) in northeastern Nebraska. *J. Paleontol.*, 45:119-121.
- WEBB, S. D. 1969. The Burge and Minnechaduzza Clarendonian mammalian faunas of north-central Nebraska. *Univ. California Publ., Geol. Sci.*, 78:1-191.
- WILSON, R. W. 1936. A Pliocene rodent fauna from Smiths Valley, Nevada. *Carnegie Inst. Washington Publ.*, 473:15-34.
- . 1939. Rodents and lagomorphs of the late Tertiary Avawatz fauna, California. *Carnegie Inst. Washington Publ.*, 514:31-38.
- . 1949. Early Tertiary rodents of North America. *Carnegie Inst. Washington Publ.*, 584:67-164.
- WOOD, A. E. 1935. Evolution and relationships of the heteromyid rodents with new forms from the Tertiary of western North America. *Ann. Carnegie Mus.*, 24:73-262.
- . 1936a. Fossil heteromyid rodents in the collections of the University of California. *Amer. J. Sci.*, 32:112-119.
- . 1936b. Geomyid rodents from the middle Tertiary. *Amer. Mus. Novitates*, 886:1-31.
- . 1937. Additional material from the Tertiary of the Cuyama Basin of California. *Amer. J. Sci.*, 33:29-43.
- WOOD, H. E., R. W. CHANEY, J. CLARK, E. H. COLBERT, G. L. JEPSEN, J. B. REESIDE, JR., AND C. STOCK. 1941. Nomenclature and correlation of the North American continental Tertiary. *Geol. Soc. Amer. Bull.*, 52:1-48.